DECISION MAKING IN FIELD CRICKETS:
FEMALE PREFERENCES, CHOICE BEHAVIOR AND UNDERLYING PROCESSING SCHEMES.

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Die Gewissheit ist mehr eine Geburt
der Unwissenheit als der Kenntnis.
- Charles Darwin

Zusammenfassung

Akustische Signale dienen vielen Tierarten als Mittel zur Partnerfindung. Oft emittieren mehrere Sender gleichzeitig ein Signal. Somit muss der Empfänger eine Wahlentscheidung treffen, auf welches Signal er reagiert, weshalb neuronale Netzwerke, welche auf das spezifische Signal abgestimmt sind, sowie Verarbeitungs- und Entscheidungsmechanismen, welche die relevanten Informationen extrahieren und integrieren um schlussendlich zu einer Entscheidung zu gelangen, nötig sind. Diese Verarbeitungsmechanismen müssen unter den Zwängen von limitierter Zeit, Prädation, schwindenden Ressourcen und akustisch diversen Umgebungen optimal funktionieren, um eine Entscheidung für den besten Paarungspartner zu treffen.

Feldgrillen sind ein hervorragendes Modellsystem zur Quantifizierung von Verarbeitungs- und Entscheidungsmechanismen im Rahmen akustischer Kommunikation, da die Wiedergabe männlicher Gesänge zuverlässig positive Phonotaxis auslöst. Durch Verhaltensexperimente können die akustischen Präferenzen der Weibchen für die verschiedenen Merkmale des männlichen Gesangs im Detail durch verschiedene Testdesigns untersucht werden und somit Rückschlüsse auf die neuronale Verrechnung gezogen werden. Bei den Feldgrillen produziert das Männchen einen Lockgesang und das Weibchen muss den arteigenen Lockgesang erkennen und lokalisieren, um sich dem Männchen mittels positiver Phonotaxis zu nähern. Dabei bewerten die Weibchen zum einen die Signalattraktivität anhand der zeitlichen Eigenschaften des Gesangs und zum anderen die Signalintensität, welche durch die körperlichen Eigenschaften des Männchens, sowie durch die Entfernung zum Weibchen beeinflusst wird. Da diese Eigenschaften des Gesangs nicht zwangsweise positiv korrelieren, wird die Entscheidung des Weibchens erschwert, da sich kein Männchen in einer Aggregation an singenden Männchen als überragend abheben wird.

Die vorliegende Arbeit beschäftigt sich mit der Frage, welche Algorithmen weibliche Feldgrillen nutzen um zu einer Entscheidung, sich einem Männchen zu nähern, zu gelangen und wie die relevanten Merkmale des männlichen Gesangs während des Prozesses der Entscheidungsfindung integriert werden. Dies wurde mittels ausführlichen quantitativen Messreihen in Verhaltensexperimenten mit einem Trackball-System für 6 verschiedene Arten von Feldgrillen (*Gryllus bimaculatus*, *G. firmus*, *G. staccato*, *G. personatus*, *G. texensis* und *G. rubens*) untersucht. Die Arten wurden in nicht-Wahl- und Wahlexperimenten hinsichtlich ihrer Antworten und Präferenzen für männliche Signale, welche sich in Pulsrate, Modulationstiefe, Intensität, Anordnung der Chirps während der Wiedergabe und der zeitlichen Verschiebung zweier Signale zueinander unterschieden, getestet. Des Weiteren wurde durch Transitivitätstests, in denen jeweils zwei Merkmale des männlichen Gesangs (1: Pulsrate/ Intensität, 2: Chirprate/ Intensität, 3: Pulsrate/ Chirprate) variiert wurden, untersucht, ob dem Wahlverhalten weiblicher Grillen rationale oder vergleichende Entscheidungsmechanismen zugrunde liegen.

Zusammenfassend zeigen die Ergebnisse, dass die Verarbeitungsmechanismen, welche der Entscheidungsfindung bei weiblichen Feldgrillen zugrunde liegen, in den untersuchten Arten ähnlich sind. Signale aus verschiedenen Richtungen werden separat durch bilateral gepaarte Netzwerke in parallelen neuronalen Bahnen für Signalattraktivität und

Signalintensität analysiert. Ein nachfolgender Verstärkungsmechanismus fusioniert die Ausgabe beider neuronaler Bahnen und die Signalintensität wird durch die Signalattraktivität gewichtet. Somit ist der Einfluss der Intensität nicht linear und die Lokalisierung des Signals nicht unabhängig von der Erkennung des Signals. Ein Vergleich der Informationen des linken und rechten Netzwerkes führt zu einer Richtungsentscheidung. Neben diesem generellen Verarbeitungsschema wurden zwischen den einzelnen untersuchten Arten charakteristische Unterschiede in der Mustererkennung, der Verarbeitung der Signalintensität und der Intensitätsgewichtung festgestellt. Nah verwandte Arten wiesen jedoch ähnlichere Präferenzen auf, als nicht nah verwandte Arten. Die Tests zur Transitivität weiblicher Präferenzen weisen auf vergleichende Entscheidungs-mechanismen hin und widersprechen einer rationalen Partnerwahl.

Schlagwörter: *Gryllus*, akustische Kommunikation, Phonotaxis, vergleichende Entscheidungsfindung, Verstärkungsmechanismus

Abstract

In many animals acoustic signals serve for mate attraction. Often several sender display their signal at the same time. Thus, the receiver has to make a decision and choose a sender, wherefore neuronal networks tuned to the species specific song and processing mechanisms which extract the relevant information are necessary. These processing mechanisms have to operate optimally under the constraints of restricted time, predation, diminishing resources and acoustically diverse backgrounds to choose the best mating partner.

Field crickets are an excellent model system to study decision making mechanisms in the context of acoustic communication, as playbacks of male songs reliably elicit positive phonotaxis. By conducting behavioral experiments the acoustic preferences of females for the different cues of male songs can be quantified in detail and conclusions about the neuronal computations can be drawn. Male crickets produce calling songs and females have to recognize and localize the species specific song to approach a male by positive phonotaxis. Thereby females assess signal attractiveness by the temporal structure of the song and signal intensity, which is influenced by the physical attributes of a male and by the distance to the female. The parameters of a calling song are not necessarily positively correlated and no male will emerge as superior in an aggregation of singing males.

The present thesis addresses the question on which cues decision making is based and how these relevant cues of a male's song are integrated during the decision process. To this aim comprehensive quantitative test series with 6 species of field crickets (*Gryllus bimaculatus*, *G. firmus*, *G. staccato*, *G. personatus*, *G. texensis* and *G. rubens*) were conducted. Using a trackball system no-choice and choice experiments were performed which systematically varied pulse rate, modulation depth, intensity, chirp/trill arrangement and temporal shifts of synchronously presented signals. Furthermore, tests for transitivity of preferences which varied two parameters of male songs (1: pulse rate/ intensity, 2: chirp rate/ intensity, 3: pulse rate/ chirp rate) in choice tests examined if female choice behavior is based on rational or comparative decision making mechanisms.

In summary, the results reveal that sensory processing underlying female decisions is similar in the six species studied here. Incoming signals from different directions are analyzed separately in bilaterally paired networks with parallel pathways for signal attractiveness and signal intensity. A downstream gain-control mechanism fuses the outcome of both pathways and signal intensity is weighted by pattern attractiveness. Therefore localization is not independent from signal recognition. Despite this general scheme remarkable characteristic differences between species were observed in pattern recognition, processing of signal intensity and weighting of signal intensity. Closely related species exhibited more similar preferences than unrelated species. Furthermore the tests for transitivity of preferences indicated that females use comparative decision making mechanism and contradicted rational mate choice.

Keywords: *Gryllus*, acoustic communication, phonotaxis, decision making, gain-control mechanism

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1. Introduction

Decision making in mate choice. Animals have to make decisions every day. Decisions are a result of an evaluation of possible options (Stevens 2008). They often begin with a goal or task and the underlying mechanism gathers and processes the available information to attain a decision and this results in an action and payoff outcome (Stevens 2008). Traditionally decision making in animals is studied from the viewpoint that animals strive to optimize their energy input and reproduction and therefore adopted their choice behavior (Kalenscher & Wingerden 2011).

Mate choice is one of the main decision-making tasks a sexually reproducing animal has to solve (Miller & Todd 1998). This includes perceiving sexual cues that provide information about a potential partner, judge overall sexual attractiveness by integrating the cues and estimating the underlying trait values and searching through several available mates to decide which one to court or to accept (Miller & Todd 1998, Fig. 1.1). Thus mate choice can be viewed as an information processing chain resulting in a decision (Fig. 1.1). But sexual displays often involve many different signal components which may provide information about different underlying qualities (Candolin 2003). If these qualities are not positively correlated females need to trade off these attributes in males (Bateson & Healy 2005).

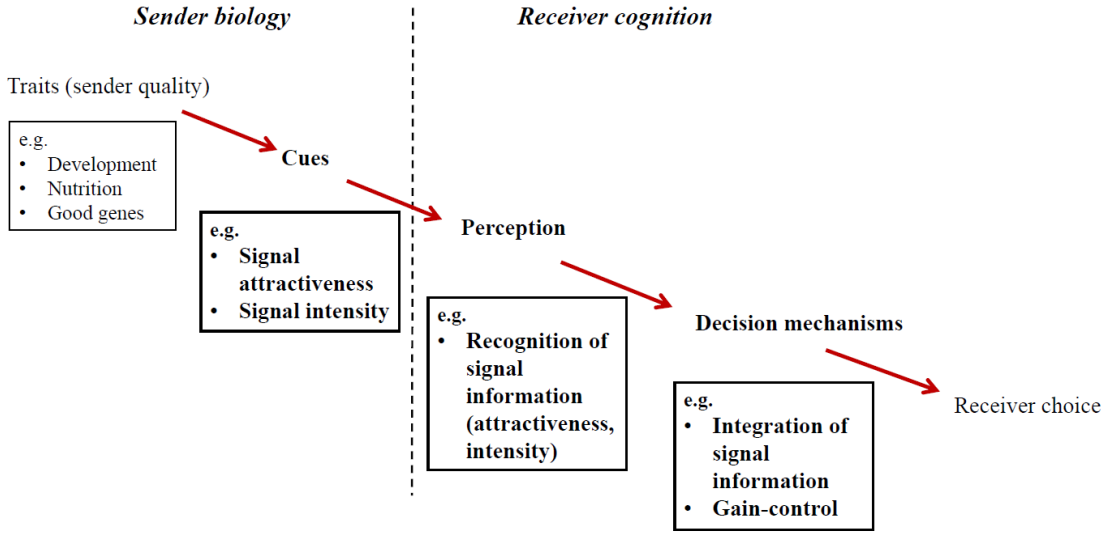

Fig. 1.1: Flow of signal information from the sender to the receiver. The cues of a sender, which are influenced by his quality, are perceived by the receiver and integrated to make a decision. Modified from Bateson & Healy 2005.

Mammals, birds, amphibians and insects use acoustic signals with variations in sound frequency, amplitude and temporal structure for mate selection and pair formation (Searcy & Andersson 1986, Webster & Fay 1992, Catchpole & Slater 1995, Gerhardt & Huber 2002). Thereby intraspecific communication critically affects reproductive success in both, sender and receiver (Gerhardt & Huber 2002). The sender transmits information and the receiver evaluates this information during decision making (Schaefer 2010, Fig. 1.1). This requires mechanisms of sound production which ensure a reliable encoding of information about the sender in the signal and the transmission over a distance to the receiver on the sender side (Gerhardt & Huber 2002). On the receiver side neuronal networks tuned to the species specific song and processing mechanisms which extract the relevant information are necessary (Gerhardt & Huber 2002). Thus several fundamental questions regarding sensory perception and decision making arise which will be addressed in the present thesis: Which are the relevant cues for mate choice? How are they weighted and integrated to arrive at a decision and what are the underlying algorithms of sensory processing?

Most studies on mate choice assume that females evaluate male attributes based on an absolute standard and act rational by choosing the male with the highest absolute score. Therefore options or males are evaluated independently and their value is not affected by the presence or absence of other options (Shafir et al. 2002). Furthermore this implies that available options (A, B, C) should be ranked in a transitive mode by the decision maker (Shafir et al. 2002) meaning that a decision maker prefers option A over option B, option B over option C and thus option A over option C (Shafir 1994, Fig. 1.2.). However studies in humans (Tversky 1969, Wedell 1991, Stanovich 2013), bees (Shafir 1994, Shafir et al. 2002, Shafir & Yehonatan 2014) and birds (Waite 2001a, 2001b, Bateson 2002, Bateson et al. 2002, 2003) showed choice behavior which was not consistent with a transitive choice and an absolute evaluation of options. Here decisions seem to be based on a comparative evaluation (Bateson & Healy 2005, Fig. 1.2) which means that the different dimensions of each option are compared with each other (Shafir & Yehonatan 2014). Nevertheless most of the mentioned studies in animals examined decision making in the context of foraging. But Bateson & Healy (2005) argue that it is likely that a comparative evaluation of mates also evolved as a mate choice mechanism because often more than one male is present displaying multi-component signals and forcing a female to choose between several males.

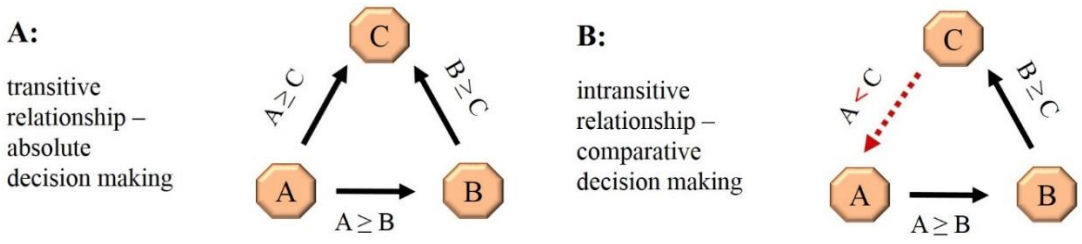

Fig. 1.2: Scheme of transitive and intransitive relationships. A Transitive relationship. Option A is preferred/ equal to option B, option B is preferred/ equal to option C and thus option A is preferred/ equal to option C. **B** Intransitive relationship – violation of transitivity if option C is preferred to option A.

Insects provide suitable systems to study decision making mechanisms that underlie mate choice in the context of acoustic communication. Many insects produce stereotypic signals with a specific temporal pattern which is a key feature for species recognition. Moreover communication develops in the absence of learning which ensures that the diversity between and within species is not a result of individual differences caused by different acoustic experiences (Pollack 2000, Gerhardt & Huber 2002). Mechanisms underlying signal production, recognition and localization can be well studied using neurophysiological experiments and behavioral playback tests that reliably elicit phonotaxis.

The cricket as a model system. Field crickets are an excellent model system to study decision making mechanisms using behavioral test paradigms. Only males produce a calling song with a species specific temporal pattern whereas sexually receptive females respond to these calls by positive phonotaxis. Male crickets produce sound by rubbing a scraper (plectrum) on the upper side of one wing against a file (elytron) with stridulatory teeth on the lower side of the other wing (Gerhardt & Huber 2002). Thereby the sound is generated during the closing movement of the wings wherefore the calling song does not consist of a continuous tone (Pfau & Koch 1994) but of a rather simple train of pulses and pauses building the species-specific temporal pattern. Every closing movement produces a pulse which consists of short oscillations representing the carrier frequency of the song.

Most crickets can be classified into two groups regarding the structure of their calling song. Some species produce pulses that are grouped into chirps and other species produce long trills with more than 20 pulses (Fig. 1.3). The temporal pattern consists of two periods, the pulse period and the chirp or trill period (Fig. 1.3). A pulse period is made up of a pulse duration and a pulse pause. The chirp or trill period is subdivided in a chirp or trill duration and a chirp or trill pause (Fig. 1.3). Other temporal parameters can be calculated using the previously mentioned acoustic properties (Fig. 1.3). The pulse rate, calculated by $1/pulse\ period$, gives the pulses per second and is a relevant cue for species recognition in many cricket species (Hennig 2009, Rothbart & Hennig 2012, Blankers et al 2015, Fig. 1.3). A division of the chirp/ trill duration by the chirp/ trill period results in the chirp/ trill duty cycle which is also a crucial parameter influencing the preference range of females (Grobe et al. 2012, Blankers et al. 2015, Hennig et al. 2016, Fig. 1.3).

The intensity of the signal can be described by the sound amplitude as given by the peak level and by sound energy over time. Sound energy can be influenced by changing the modulation pattern. A decrease in modulation depth of the pulse pauses will increase signal energy, but will also affect the attractiveness of the signal (Fig. 1.3).

All of these measures in principle describe the available cues on which females can base a decision.

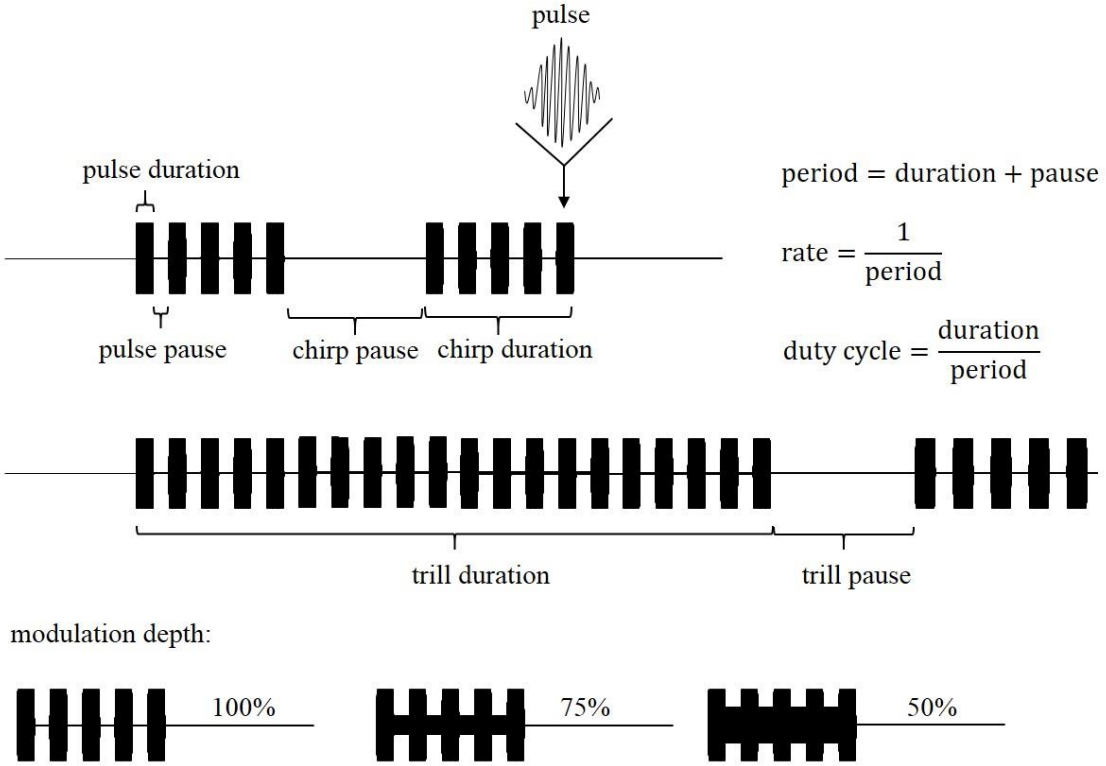

Figure 1.3: Schematic illustration of male calling songs for chirping and trilling crickets. Computational measures of temporal parameters; period, rate, duty cycle and illustrative examples of different modulation depths of the pulse pauses.

To approach a male a female has to recognize the species specific song pattern and to localize the sound source (Fig. 1.1). Therefore three steps of processing occur in the auditory pathway of insects which are the processing of frequency, temporal pattern and directional information (Hennig et al. 2004). At the stage of frequency processing the species specific carrier frequency of a male calling song is detected. Thus it gives initial information about 'who' is calling (Pollack 2000). Temporal processing provides information about the kind and content of a signal and is relevant for recognition of the species specific song (Hennig et al. 2004). Thus most information about the 'what' of a signal (Pollack 2000) is extracted from the envelope of the acoustic signal (Hennig et al. 2004). Processing of directional information provides 'where' the signaler is located (Pollack 2000, Hennig et al. 2004). The cues for localization are the interaural differences (time or phase and intensity differences) in tympanal vibrations of a pressure gradient receiver (Stumpner & von Helversen 2001, Hennig et al. 2004).

So far several studies in the past addressed the question which cues of male songs are crucial for a female to recognize and approach a male (Popov & Shuvalov 1977, Wendler 1989, Stabel et al. 1989, Doherty 1985a, 1985b, 1991, Doherty & Storz 1992, Hennig & Weber 1997, Hennig 2003, Kostarakos et al. 2008, 2009, Trobe et al 2011, Schneider & Hennig 2012, Grobe et al. 2012, Meckenhäuser et al. 2013; Blankers et al. 2015, Hennig et

al. 2016). Most of these studies tested the sensitivity of females for a variation of the cues of male calling songs in isolation (but see Doherty 1985a, Pollack 1986, Doherty & Storz 1992). However it is a common problem in nature that animals need to select and orient toward one out of several signals arriving more or less simultaneously from spatially different sources (Gerhardt & Huber 2002). Crickets often sing in aggregations (Cade 1981, Simmons 1988) and therefore a female may be in an earshot array of several males singing at the same time from different distances and directions. Thus the female is confronted with the problem of recognizing and localizing a single signal out of a complex acoustic background (Pollack 2000), a situation not unlike the human cocktail party problem (Cherry 1953, Bee 2008, Bee & Micheyl 2008). Therefore the neural analysis of pattern recognition and localization must somehow be integrated or coordinated for a decision (Gerhardt & Huber 2002, Fig. 1.1).

It is a much debated issue whether pattern and directional information are processed in a serial or parallel pathway in the neuronal system of crickets. On the one hand peripheral cues like differences in intensity and the timing of pulses will influence the turning response and on the other hand the pattern attractiveness or quality will play an important role in the decision process (Fig. 1.1). According to earlier proposals by Wendler (1989) and Stabel et al. (1989) female crickets will turn towards the side where a pattern is represented with a better quality and thus the processing of pattern and directional information is performed in a serial pathway. Moreover Pollack (1986) found that female crickets are able to distinguish between two different attractive song patterns played simultaneously from either side. This view is supported by bilaterally paired neurons selective for pulse rate (Kostarakos & Hedwig 2012, Schöneich et al. 2015). Furthermore, a male's calling song is composed of temporal and spectral properties which can be varied independently and singing from different distances results in varying intensities perceived by a female. The temporal and the intensity cues are not necessarily correlated which forces the female to trade-off male attributes to make a decision. Thus no male will emerge as superior wherefore decision making in crickets may be based on a comparative evaluation of the males rather than on an absolute evaluation. This would also favor a serial processing of acoustic information as a comparative evaluation of males is not possible, if pattern and directional cues are processed independently as for instance in grasshoppers (von Helversen 1984, von Helversen & von Helversen 1995). Nevertheless the proposal of a serial processing was also challenged by Hedwig and Poulet (2004, 2005; Poulet & Hedwig 2005) claiming that phonotactic behavior emerges from reactive steering and their behavioral data refute the proposed serial organization of pattern recognition and localization.

The scope of the thesis. The aim of this thesis was to comprehensively understand how female crickets arrive at their decision to choose and approach a male and particularly how different cues of male calling songs are integrated and processed in the neuronal system. A lot of work has been done in the past to examine the relevant cues that elicit positive phonotaxis in females. However, here the contribution of specific cues to decision making in no-choice and especially choice situations will be investigated. Furthermore it will be examined if the information flow underlying decision making is similar in different cricket species and if the scheme of auditory processing that integrates the different cues is generalizable between species. To this end, behavioral experiments with female crickets were performed on a trackball system.

First the impact of pattern attractiveness and sound amplitude on female preferences for acoustic signals in no-choice and choice situations was examined (**2.1.**, Gabel et al. 2015). The outcome of no-choice and choice experiments was compared and female choice behavior was predicted using a simple computational model. Furthermore different schemes of auditory processing which could underlie female choice behavior were discussed here.

In the next step the relative contribution of relevant cues for female choice (pattern attractiveness and signal intensity) to decision making in crickets was investigated (**2.2.**, Gabel et al. submitted). Therefore a series of no-choice and choice experiments systematically varying pattern attractiveness and sound amplitude or sound energy was conducted. Using these results an equivalence function was constructed which examined the relative contribution of both cues to female decisions.

As the previously mentioned studies were performed on female *Gryllus bimaculatus* the next study dealt with female preferences for male acoustic signals and choice behavior in five other species of field crickets to determine common features or differences in the weighting of cues and the scheme of auditory processing in crickets. Therefore no-choice and choice experiments varying pulse rate, modulation depth, intensity, chirp/trill arrangements and temporal shift between two patterns were performed with female *Gryllus firmus*, *G. "staccato"*, *G. personatus*, *G. rubens* and *G. texensis* (**2.3.**, Gabel et al. submitted).

Finally it was tested if female crickets evaluated the calling songs based on absolute or comparative decision making mechanisms. Therefore females were tested for transitivity of preferences by conducting a series of binary choice experiments and comparing these results to female preferences in no-choice experiments (**2.4.**, Gabel & Hennig 2016).

2. Manuscripts

2.1.
Decision making and preferences for acoustic signals in choice situations by female crickets.

E. Gabel, J. Kuntze & R.M. Hennig (2015) Decision making and preferences for acoustic signals in choice situations by female crickets.
Journal of Experimental Biology 218, 2641-2650
doi: 10.1242/jeb.120378

The aim of this study was to examine how different cues of male calling songs are weighted for a decision by female crickets *Gryllus bimaculatus*. We conducted choice experiments presenting two songs with different temporal patterns and/or signal intensities using a trackball-system and compared the outcome with results of no-choice experiments. Furthermore we developed a simple computational model to predict female choice behavior and compared possible schemes of processing of acoustic signals.

The results of the study are:

1. If two patterns were presented at equal sound intensity preference functions for acoustic signals became wider in a choice situation compared to a no-choice situation.

2. If stimuli in choice tests were presented at different sound intensities this effect was counteracted and preference functions became narrower compared to the equal sound intensity situation.

3. The weighting of sound intensity depended on the temporal pattern and was nonlinear.

4. A computational model based on the temporal pattern and on sound intensity reliably predicted female choice behavior.

5. The analysis of pattern recognition and directionality is performed in separate neuronal pathways with parallel topology but the computational flow of information corresponds to a serial processing.

2.2.
A gain control mechanism governs the weighting of acoustic signal intensity and attractiveness during female decisions.

E. Gabel, P. Vural, L. Mariot & R.M. Hennig (2016) A gain control mechanism governs the weighting of acoustic signal intensity and attractiveness during female decisions. *Animal Behaviour* 122, 197-205
http://dx.doi.org/10.1016/j.anbehav.2016.10.019

In this study we investigated how female crickets *Gryllus bimaculatus* integrate pattern attractiveness and signal intensity as given by sound amplitude or sound energy during decision making. First we conducted no-choice experiments to determine female response functions for pattern attractiveness and signal intensity. Second pattern attractiveness and sound amplitude or sound energy were systematically varied in a choice-paradigm. From both datasets we constructed an equivalence function for pattern attractiveness and signal intensity to examine the relative contribution of both cues to decision making.

The results of the study are:

1. For patterns of high attractiveness there was a strong influence of even small intensity differences on female choice behavior, but patterns with low attractiveness required large intensity differences to influence female decisions to their favor.

2. The integration of pattern attractiveness and signal intensity is provided by a gain-control mechanism which leads to a nonlinear weighting of signal intensity by pattern attractiveness.

3. Sound amplitude and sound energy showed the same dependence in the equivalence function and therefore it is likely that both are processed at the same station in the peripheral auditory network.

2.3.
How females of chirping and trilling field crickets integrate the 'what' and 'where' of male acoustic signals during decision making.

E. Gabel, D.A. Gray & R.M. Hennig (2016) How females of chirping and trilling field crickets integrate the 'what' and 'where' of male acoustic signals during decision making. *Journal of Comparative Physiology A* 202(11), 823-837
doi: 10.1007/s00359-016-1124-x

Here we aimed to examine how pattern attractiveness and signal intensity are integrated during decision making in five species of chirping and trilling field crickets (*Gryllus firmus*, *G. "staccato"*, *G. personatus*, *G. rubens* and *G. texensis*). Using a trackball-system we conducted no-choice and choice experiments testing each species for their responses to song patterns with different pulse rates, modulation depths, intensities, chirp/trill arrangements and temporal shifts of synchronously presented signals. We compared the outcome of the experiments and the relative contribution of pattern attractiveness and signal intensity to decision making between species and discussed the results in the context of neurobiological mechanisms as well as phylogeny and ecology of the acoustic communities.

The results of the study are:

1. The sensory processing underlying decision making in female field crickets is similar in all chirping and trilling species.

2. Pattern attractiveness and signal intensity are processed by separate neuronal pathways in bilaterally paired networks but a gain-control mechanism fuses their outcome and leads to a weighting of signal intensity by pattern attractiveness.

3. Remarkable differences between species were observed with respect to specific processing steps, but closely related species showed more similar preferences than distantly related species.

2.4.
Evidence for comparative decision making in female crickets

E. Gabel & R.M. Hennig (2016) Evidence for comparative decision making in female crickets.
Behavioral Ecology (2016) 00(00), 1-7
doi: 10.1093/beheco/arw030

In this study we tested the transitivity of preferences of female crickets *Gryllus bimaculatus* for male calling songs in order to investigate if females evaluate male signals based on absolute or comparative decision making mechanisms. Therefore we conducted a series of binary choice experiments using a trackball-system and compared their outcome to female preferences exhibited in no-choice experiments. Every choice pair had to differ in two parameters to test for transitivity. We used the following parameter pairs and kept all other parameters constant: (1) pulse rate and sound intensity, (2) chirp rate and sound intensity, (3) pulse rate and chirp rate.

The results of the study are:

1. Females acted transitively if chirp rate and sound intensity or pulse rate and chirp rate of male signals were varied.

2. Females violated transitivity if pulse rate and sound intensity of male signals were varied.

3. The results suggested a comparative evaluation of male signals by female crickets as violations of transitivity occurred.

3. General Discussion

This thesis addressed the integration of the cues of male calling songs and the decision process underlying choice behavior in female crickets. Therefore the effect of different cues of male calling songs on female choice behavior was measured in single stimulus and two choice experiments and the findings were related to the computational flow of information.

Sensory bias, information flow and algorithms of decision making. The studies presented here demonstrate that the sensory processing underlying decision making in female crickets is similar in six species of field crickets. Nonetheless characteristic differences between species were observed while closely related species exhibited more similar preferences than distantly related species.

All species evaluated pulse rate and modulation depth for the attractiveness of the temporal pattern and sound amplitude and sound energy as given by the modulation depth for signal intensity [2.1, 2.2, 2.3]. *G. bimaculatus*, *G. firmus*, *G. rubens* and *G. texensis* showed closed response functions for pulse rate with a peak preference at their species typical pulse rate ([2.1, 2.2, 2.3, 2.4], Fig. 3.1). *G. personatus* exhibited a peak preference at their species typical pulse rate but also responded well to higher pulse rates [2.3]. *G. "staccato"*, however, showed a high responsiveness at pulse rates equal to or higher than the species typical level ([2.3], Fig. 3.1). *G. bimaculatus*, *G. firmus*, *G. rubens* and *G. texensis* were sensitive to changes in modulation depth and showed increasing responses with increasing modulation depth ([2.2, 2.3], Fig. 3.1). In contrast *G. "staccato"* and *G. personatus* tolerated all modulation depths ([2.3], Fig. 3.1). The type of chirp arrangement which could have an effect on pattern attractiveness if patterns were superimposed externally or internally or were internally pooled, showed no effect on female turning responses ([2.1, 2.3], Fig. 3.1) which confirms the view that crickets form acoustic hemispheres (Pollack 1986, 1988, Römer & Krusch 2000) and incoming patterns are analyzed by two bilaterally paired networks (Pollack 1986, 1988, [2.1, 2.2, 2.3]). This is supported by the results of Brunnhofer et al. (2016) who demonstrated spatial release from masking in *G. bimaculatus*. For spatial release from masking a separate bilateral representation of incoming signals is a requirement as only then the masker and the signal are represented separately (Brunnhofer et al. 2016).

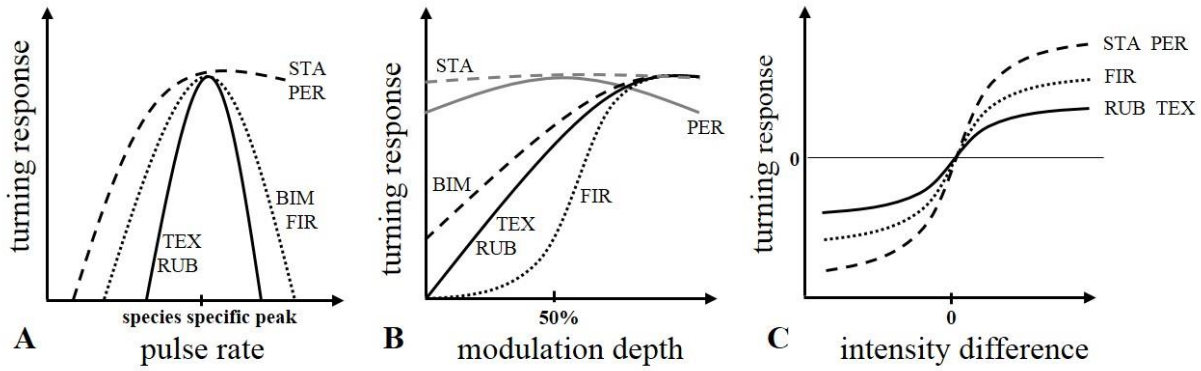

Fig. 3.1: Schematic illustration of female response functions for *G. "staccato"* (STA), *G. personatus* (PER), *G. firmus* (FIR), *G. bimaculatus* (BIM), *G. texensis* (TEX) and *G. rubens* (RUB). **(A)** Schematic response functions for a variation of pulse rate in a no-choice situation. TEX, RUB, BIM and FIR exhibited closed response function whereby TEX and RUB showed more selective preferences. STA and PER showed open response functions. To simplify, no distinction was made at which specific pulse rate the different species exhibited their peak preference. **(B)** Schematic response functions for a variation in modulation depth of the pulse pauses. **(C)** Schematic response functions for different chirp and trill arrangements (simultaneous, alternating, interleaved) at increasing intensity differences. All chirp and trill arrangements led to similar intensity dependent responses in all species wherefore only one function is shown for each species. Thereby the response level was highest for STA and PER, intermediate for FIR and lowest for RUB and TEX.

The bilaterally paired networks process pattern attractiveness and signal intensity of the incoming signals separately in parallel neuronal pathways [2.1, 2.2, 2.3] as pattern recognition with respect to pulse rate and modulation depth was intensity invariant in no-choice experiments except for *G. "staccato"* and *G. personatus* at high pulse rates [2.1, 2.2, 2.3]. In contrast in choice situations signal intensity had a strong influence on female decisions [2.1, 2.2, 2.3]. The choice experiments with differences in signal intensity in 2.1 – 2.3 and the equivalence functions [2.2, 2.3] revealed the presence of a gain-control mechanism which fuses the outcome of the parallel pathways and led to a weighting of signal intensity by pattern attractiveness. Hence localization is not independent from pattern recognition in crickets as it is the case in grasshoppers (von Helversen & von Helversen 1995).

Even if song recognition and an intensity dependent localization take place in separate parallel pathways, pattern and directional information are not processed completely independent as the gain-control mechanism fuses the outcome of the parallel pathways. This corresponds to a serial operation, although this processing scheme differs from earlier proposed simple schemes of serial processing of auditory information which suggested two bilaterally paired recognizers which evaluate pattern attractiveness and intensity in the same pathway (Stabel et al. 1989, Wendler 1989, von Helversen & von Helversen 1995). As

Wendler (1989) and Stabel et al. (1989) stated crickets should not only turn towards the louder pattern but also towards the better pattern. If two equally attractive patterns were presented at equal intensity females did not prefer one of both which is consistent with the results found by Wendler and other earlier results ([2.1, 2.2, 2.3]; Doherty 1985a, Weber & Thorson 1988, Wendler 1989, Stabel et al. 1989, Doherty & Storz 1992). Furthermore females were able to track a softer more attractive pattern in the choice experiments done here [2.1, 2.2, 2.3, 2.4] as it was also found in other studies (Doherty 1985a, Doherty & Storz 1992) and which is consistent with the statement that females track a course were the signal is presented with a better pattern (Wendler 1989, Stabel et al. 1989). Thus in a choice situation a comparison between the information from both sides leads to a directional decision.

Nevertheless differences to the results of Wendler (1989) were found here. In his experiments female *G. campestris* did not track an unmodulated tone if presented alone. If the tone was presented in competition to a calling song females chose a direction with a component towards the calling song but away from the continuous tone (Wendler 1989). The results presented here demonstrated that this did not apply for all species [2.2, 2.3]. For *G. firmus*, *G. rubens* and *G. texensis* unmodulated tones were also unattractive and they showed no response in no-choice situations [2.3]. But in contrast *G. "staccato"* and *G. personatus* showed high responses to patterns without a pulse modulation [2.3]. *G. bimaculatus* also exhibited significant responses in a no-choice situation [2.2] and an unmodulated tone had an impact on female turning responses in a choice situation [2.1]. In a choice situation *G. "staccato"* and *G. personatus* even preferred patterns with low modulation depths over a pattern with 100% modulation [2.3]. This is due to the twofold influence of a variation in modulation depth. On the one hand modulation depth acts on pattern recognition and influences pattern attractiveness; on the other hand it also influences the processing of intensity as with decreasing modulation depth the energy of the signal increases [2.2, 2.3]. Thus for *G. "staccato"* and *G. personatus* low modulation depths even enhance the attractiveness of a pattern as patterns with low modulation depths were preferred over a pattern with 100% modulation in choice situations because of their higher signal energy. This contradicts the results of Wendler (1989) as he found a negative influence of the unmodulated tone on female phonotaxis. Female *G. campestris* walked away from the tone (Wendler 1989). *G. "staccato"* and *G. personatus* surely represent extreme cases, but also *G. bimaculatus* and *G. texensis* showed a preference for a pattern with a lower modulation depth over a pattern with 100% modulation [2.2, 2.3].

Nevertheless in the experiments done here signals without a pulse modulation had a chirp structure which probably was not the case in the experiments of Wendler (1989). Potentially this is a further reason for the detected differences, as a continuous tone without pulse and chirp structure should not evoke positive phonotaxis.

To conclude the results of 2.1, 2.2 and 2.3 demonstrated a hemispheric separation of incoming signals which are analyzed by two bilaterally paired networks with parallel pathways for pattern attractiveness and the difference in intensity as there was no external or internal superposition of signals (Pollack 1986, 1988). A downstream gain-control mechanism fuses the outcome of the parallel pathways and leads to a weighting of signal intensity by pattern attractiveness (Doherty 1985a, Poulet & Hedwig 2005). A comparison

between the left and the right network leads to a directional decision (Fig. 3.2). This sensory processing scheme is similar for the six *Gryllus* species studied here although species specific differences were found at different processing stages (Fig. 3.2, [2.3]).

This type of sensory processing is in part similar to findings in katydids but different from auditory processing in grasshoppers and from more complex representations in birds and mammals which perform an auditory stream segregation or scene analysis, all of which will be considered in the following sections (but see Schul & Sheridan 2006 for an example of auditory stream segregation in an insect in the context of predator avoidance).

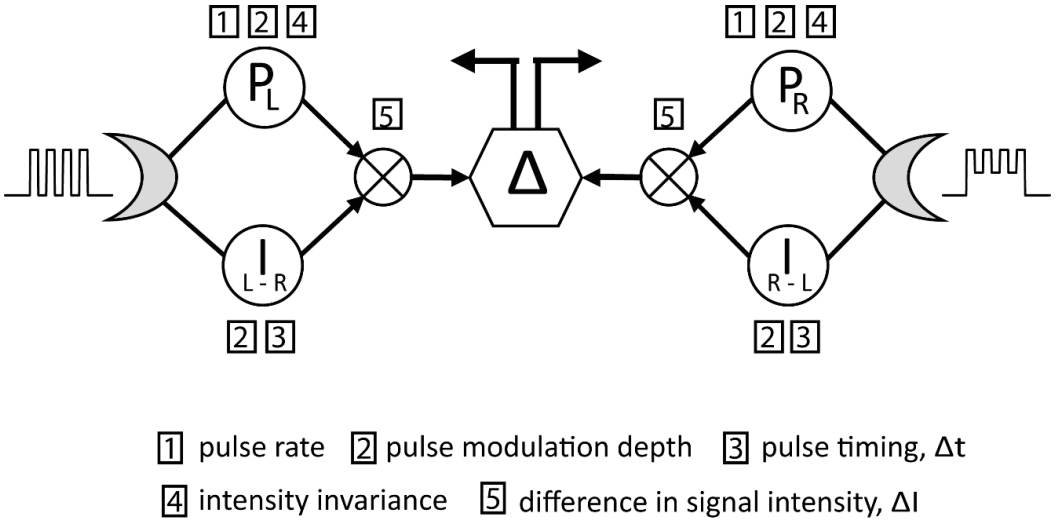

Fig. 3.2: Scheme of auditory processing with points in the processing chain marked at which differences between species were observed. Computation of pattern attractiveness and directional information. The auditory input from both sides is analyzed for the temporal pattern (P_L, P_R) and the difference in intensity (I_{L-R}, I_{R-L}). Both cues are integrated by a gain control mechanism (circles with crosses) which results in a non-linear weighting of the intensity cue by pattern attractiveness. A comparison between both sides leads to a directional decision (Δ). Taken from 2.3, same as Fig. 5 in 2.3.

A separate bilateral paired representation of auditory information received from both ears and a serial processing of auditory information was beside crickets also proposed for katydids (Schul et al. 1998, Römer & Krusch 2000; Brunnhofer et al. 2016) but is not present in all insects. In grasshoppers the input of both tympanal organs is pooled internally before it enters the process of pattern recognition which implies that song recognition takes place in a non-directional pathway and directional information are processed independently in a parallel pathway (von Helversen 1984, von Helversen & von Helversen 1995).
In frogs pattern recognition is like in crickets based on the spectral and temporal properties of male advertisement calls (Feng et al. 1990, Gerhardt & Huber 2002). The quality of the male signals affects the orienting movements as it is the case in crickets. Females of *Hyla*

chrysoscelis and *H. versicolor* preferred high call rates over slow call rates even if the sound pressure level of the preferred stimuli was attenuated by 6dB (Gerhardt et al. 1996). Similar as in crickets and katydids spatial release from masking is a potentially important mechanism for sound source segregation (Bee 2007).

In birds and also mammals information about the location of a sound source is represented in spatially organized maps in the central nervous system which was for instance shown in studies of the barn owl and bat systems (Suga 1990, Konishi 1994). In barn owls time and intensity cues are processed in separate neuronal pathways (Takahashi et al. 1984, Konishi 2003). Takahashi et al. (1984) demonstrated that time and intensity are independently processed by monitoring the activity of space-specific neurons and that the processing of one cue does not interfere with that of the other under normal physiological conditions. Thus similar to grasshoppers but in contrast to crickets intensity differences have a constant contribution to sound localization. In contrast to crickets and katydids which are known to form acoustic hemispheres (Pollack 1988, Römer & Krusch 2000) vertebrates perform an auditory scene analysis (Bregman 1993). Signal and directional information is processed separately in the auditory system which allows an independent representation and accurate localization (Knudsen & Konishi 1978, Ahveninen et al. 2006, Grothe et al. 2010, Bizley & Cohen 2013).

Thus different species have evolved different solutions to be able to orient towards one of several sounds arriving from different directions. In crickets and katydids hearing and sound production may have coevolved given the background of mate attraction (Alexander 1962, Gerhardt & Huber 2002). Therefore signal processing is likely to be highly specialized and dedicated for this purpose in these families (Gerhardt & Huber 2002). A dependent computation of pattern and directional information has several advantages for a signal receiver living in a highly noisy social background. Females are able to first analyze the attractiveness of the perceived male songs before choosing one male and approaching the male (Gerhardt & Huber 2002). The gain-control mechanism seems to be one adaptive solution to detect species specific signals and discriminate between several variants of conspecific songs (Brunnhofer et al. 2016) and is potentially able to facilitate the detection and discrimination between several different conspecific and heterospecific song signals (Gerhardt & Huber 2002).

From economics to mating decisions. Traditionally studies on mate choice assumed that females decide rationally (Ryan et al. 2009). Thus they transduce all male cues into one single preference score which is independent of the scores of other potential mates and choose the male with the highest absolute score (Ryan et al. 2009). In contrast Bateson & Healy (2005) argued that comparative decision making mechanisms which were known for foraging behavior in animals could also have evolved in the context of mate choice. The results of the tests for transitivity presented here [2.4] demonstrated that females evaluate male calling songs based on relative instead of absolute standards. The same was suggested by Hirtenlehner (2014) for *Gryllus bimaculatus* who tested the second concept besides the principle of transitivity to proof rational decision making which is "the independence of irrelevant alternatives (IIA)" (Bateson & Healy 2005). The independence of irrelevant alternatives states that the addition of an inferior option to a choice set should not influence

the relative preferences between the original options (Bateson et al. 2002, Bateson & Healy 2005). Hirtenlehner (2014) presented two songs in a choice set, one less attractive than the other, and added a third different signal variant which was known to be less attractive as well to the less attractive signal. Doing so female preference for the more intense or more attractive signal of the original choice set disappeared (Hirtenlehner 2014). This violation of the IIA principle and the violation of the principle of transitivity examined in Gabel & Hennig (2016) indicate a decision making process using comparative rather than absolute decision making rules, similar to what was found in honey bees, hummingbirds, starlings, gray jays and humans (Shafir 1994, Sedikides et al. 1999, Shafir et al. 2002, Shafir & Yehonatan 2014, Waite 2001a, 2001b, Bateson et al. 2002, Bateson 2002, 2004, Morgan et al. 2012, 2014).

Comparative mate evaluation as observed here for crickets can have several advantages for males and females. It predicts that males could manipulate their attractiveness to females by choosing the appropriate social background (Bateson & Healy 2005). Male crickets could develop different strategies to maximize their success in mate attraction. They could adapt the cues of their acoustic signals to produce a more attractive song than the competitor, they could produce louder acoustic signals than the other male or could display the song at a closer distance to the female. Thus they should carefully position themselves spatially when displaying to females (Bateson & Healy 2005). Moreover for females comparative mate choice mechanisms predict that there is variation in female preference depending on the background conditions and the composition of the group of displaying males in which she evaluates the male (Bateson & Healy 2005). Therefore comparative mate evaluation causes varying mating preferences between and within species and thus may also ensure that the same male is not always chosen (Jennions & Petrie 1997, Bateson & Healy 2005).

The results of the tests for transitivity are congruent with the results of 2.1 and 2.2 for *G. bimaculatus*. Sound intensity had a different influence in no-choice and choice situations. Preferences of female *G. bimaculatus* for a variation of pulse rate were intensity invariant in no-choice situations [2.1, 2.2, 2.4]. In contrast, in choice situations signal intensity had a strong influence. At high differences in sound amplitude females preferred signals with low attractiveness over more attractive pulse rates [2.1, 2.2, 2.4] which resulted in non-transitive choices [2.4]. Nevertheless it was also observed that the softer attractive reference pattern was preferred over the louder alternative pattern [2.4] which corresponds to the results of choice experiments with differences in signal intensity in 2.1 and 2.2. Thus the results of all studies presented here regarding a variation of pulse rate and signal intensity support the presence of a gain-control mechanism in auditory processing in female crickets which leads to a nonlinear weighting of the intensity cue by pattern attractiveness [2.1, 2.2, 2.3, 2.4]. But as violations of transitivity were only found if pulse rate and intensity were varied and not if chirp rate and intensity were varied [2.4] it appears that the gain-control mechanism acted stronger on the short time scale. Already the evaluation of chirp rate was not intensity invariant in no-choice situations and in choice situations females always chose the louder pattern [2.4].

A nonlinear evaluation of different cues as it was found in the studies presented here is widespread in biological systems. In honeybees Ronacher (1979, 1980, 1983) determined a

nonlinear equivalence function for size and degree of greyness of two simultaneously presented discs. Here the shades of grey influenced choice reactions more strongly than the difference in size (Ronacher 1983). In the nectarivorous bat species *Glossophaga commissarisi* Nachev and Winter (2012) found a nonlinear evaluation of reward. They described a nonlinear increase of discrimination ability with respect to stimulus intensity which may be due to a nonlinear perception and encoding process (Nachev & Winter 2012). For the bumblebee *Bombus impatiens* Nachev et al. (2013) also found a nonlinear reward evaluation. Time perception in rats is nonlinear (Crystal 2001). Here the sensitivity to time is nonlinearly related to physical time (Crystal 2001). He suggested that the nonlinearity is introduced at a perceptual or memorial stage of processing. In humans a nonlinear processing occurs for instance in the visual system. The results of Lucassen and Walraven (1993) revealed a nonlinear response function for the input variables contrast and illumination level in which the contrast signal is not independent of luminance.

Assumed that a nonlinear processing of perceptual information is a result of natural selection it seems to be advantageous and superior to other mechanisms as it minimizes the errors in choice behavior (Sinn 2003, Portugal & Svaiter 2010, Nachev et al. 2013). Nonlinear representational mechanisms boast a certain robustness against errors. As discussed in 2.3 the nonlinear weighting of signal intensity during signal processing in crickets seems to reduce detrimental choices of patterns with low attractiveness or that is to say errors in choice behavior. It enables a preference for a softer more attractive pattern thus in the field for a male with higher quality displaying from a greater distance. Nevertheless limitations of the proposed processing scheme were observed as at very high sound intensities intransitive preferences in choice behavior occurred [2.4] and females preferred a louder less attractive pattern over a softer more attractive pattern [2.1, 2.2, 2.3, 2.4]. Such a cognitive limitation is expected to be detrimental in the context of rational choice theory but can also have advantages for the female (Kareev 2012). Females may save costs and time by approaching the louder singing male as in the field it is the male singing at a closer distance. Furthermore the time females are exposed to predators while approaching the male is reduced.

4. Outlook

The present work deals with a fundamental question in sensory perception and decision making: How are different available cues weighted during decision making and which function describes the integration of relevant cues for female decisions? What are the underlying and general computational mechanisms to arrive at a decision? To answer these questions a behavioral test paradigm was used measuring female acoustic preferences and choice behavior of field crickets in single stimuli situations and two-choice situations as both types of tests are relevant to assess the underlying mechanisms of female decisions. The comparison of both test situations and the test design allowed to draw conclusions about the neuronal computation of acoustic signals in crickets from behavioral evidence. For future research it would be interesting to confirm the behavioral data found here by conducting experiments at the neuronal level using electrophysiological methods. Linking the behavioral experiments performed here to neuronal activity would enable us to test the proposed processing scheme of recognition and localization of acoustic information. Therefore neurons of the left and right side should be recorded simultaneously in order to document the stimulus-related activity in the neurons of both sides during decision making.

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– Adolph Kolping

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Selbständigkeitserklärung

Hiermit erkläre ich, dass ich diese Dissertation selbständig und nur unter Verwendung der angegebenen Literatur und Hilfsmittel angefertigt habe. Die Dissertation ist in keinem früheren Promotionsverfahren angenommen oder als ungenügend bewertet worden. Die dem angestrebten Verfahren zu Grunde liegende Promotionsordnung erkenne ich an.

Berlin, den

Eileen Gabel